On the Distribution and Faunogenesis of Himalayan Millipedes (Diplopoda): Preliminary Results[1]

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ABSTRACT

The fauna of Diplopoda of the Himalayas (over 200 species, mostly endemic) is reviewed, with particular reference to that of their central part. In spite of the preliminary state of knowledge, the patterns of vertical and geographic distributions suggest the fauna to be eventually entirely Oriental and/or Indian in origin, and primarily associated with forest tropical and/or subtropical communities. The so-called Palearctic influence in the relatively well-explored Central Himalayas actually also originates in the present-day subtropical regions of Southeast and East Asia. The Himalayas seem to have served as a pathway for repeated spreads of a uniform Turgai biota (with Diplopoda being an accompanying group) which, chiefly during the early and middle Tertiary, advanced northwestward, following the receding southern coast of the Tethys Sea. Naturally, during their relatively short orogenic history, the Himalayas also served as a major center of secondary diversification for numerous groups, especially during the Plio-Pleistocene.

RÉSUMÉ

Répartition et genèse des faunes de Diplopodes de l'Himalaya : résultats préliminaires.

La faune des diplopodes des massifs himalayens (plus de 200 espèces, la plupart endémiques), plus particulièrement de leur partie centrale, est révisée. Les modalités de la répartition verticale et géographique suggèrent pour cette faune une origine entièrement orientale et/ou indienne, primitivement associée à des peuplement forestiers tropicaux et/ou subtropicaux. L'influence dite paléarctique provient, dans les régions relativement bien explorées des chaînes centrales de l'Himalaya, des aires subtropicales actuelles du Sud-Est et de l'Est asiatique. Les massifs himalayens semblent avoir servi de "bordure" à des extensions répétées d'un type d'écosystème uniforme de type "Turgai" (les diplopodes apparaissant comme un groupe accompagnateur) qui, surtout durant le début et le milieu de l'ère tertiaire, a progressé vers le Nord-Ouest à la suite du recul de la côte méridionale de la Téthys. Bien entendu, durant cette histoire orogénique relativement courte, les massifs himalayens ont été également un centre majeur de diversification secondaire pour de nombreux groupes d'êtres vivants, notamment au cours du Plio-Pléistocène.

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1 Results of the Himalaya Expeditions of J. Martens, No. 201. — For No. 200 see: Bonner Zoologische Monographien, 39, 1995. — J. M. sponsored by Deutscher Akademischen Austauschdienst, Deutsche Forschungsgemeinschaft and Feldbausch Foundation, Fachbereich Biologie, Universität Mainz.

GOLOVATCH, S. I. & MARTENS, J., 1996. — On the distribution and faunogenesis of Himalayan millipedes (Diplopoda): preliminary results. *In*: GEOFFROY, J.-J., MAURIÈS, J.-P. & NGUYEN DUY - JACQUEMIN, M., (eds), Acta Myriapodologica. *Mém. Mus. natn. Hist. nat.*, **169** : 163-174. Paris ISBN : 2-85653-502-X.

INTRODUCTION

Being one of the globe's greatest mountainous lands supporting the highest peaks such as Everest, Kanchenjunga, Manaslu, Annapurna, etc., the Himalayas occupy a vast area encompassing the ranges lying between the rivers Indus and Brahmaputra and roughly delimited by 74°E in the west and 95°E in the east (Fig. 1). The adjacent Karakorum and Kohistan-Baluchistan regions in the west, and the Arakan-Chin-Yoma fold belt and the Magok belt in the east are of the same orogenesis (MASCLE *et al.*, 1990).

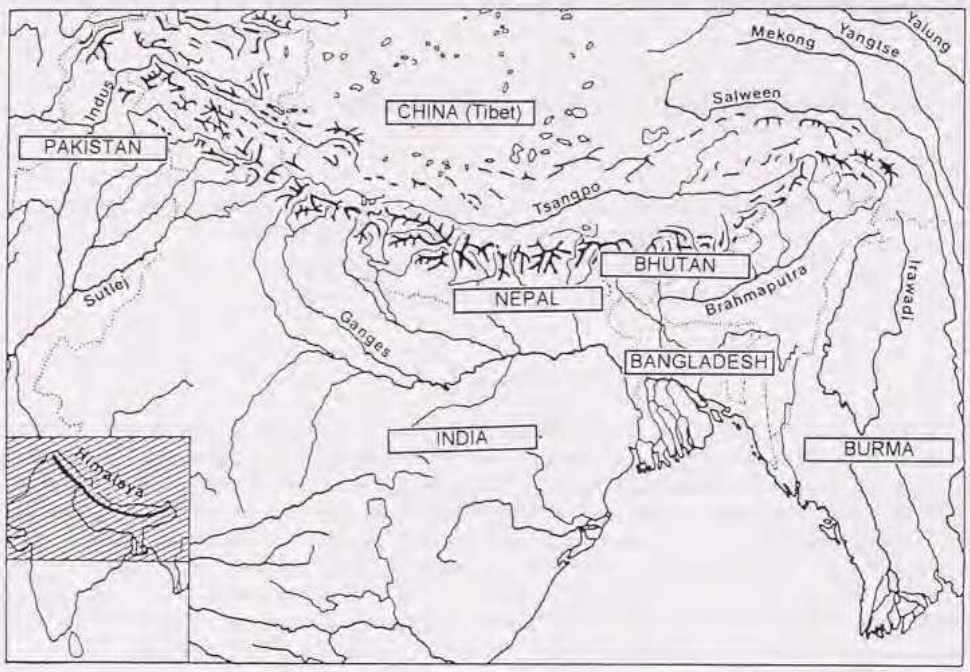

FIG. 1. — Orography of the Himalayas.

From a biologist's viewpoint, the Himalayas represent a highly important barrier between the cold and arid uplands of Central Asia and largely tropical South and Southeast Asia, reinforcing the contrast and, in spite of numerous local inversions, creating their own climate. During the southwestern monsoon period, precipitation mainly occurs on the southern slopes, being greatly reduced on the northern ones. However, this barrier function holds true only for the central parts of the mountains, more or less within Kumaon, Nepal, Sikkim, and Bhutan. In the western Himalayas, the aridity of Central Asia extends across the southern slopes, while in the eastern parts rainstorms, though declining in amount and frequency, reach as far as Southeast Tibet (TROLL, 1967).

This drastic climatic gradient within the Central Himalayas is of great importance, influencing the distribution of various organisms. Although phyto- and zoogeographic regions differ in certain details, both emphasize the role of the Himalayas as a contact region between two great biogeographic realms, the Palearctic and Oriental, which meet and intermesh there in various ways. All areas north of the Central Himalayas obviously belong to the Palearctic, as do the highest parts of the inhabited southern flanks. The lower and lowest altitudes of the southern slopes are largely attributable to the Oriental realm. However, the border between both regions is generally neither striking nor abrupt, forming more (especially in the eastern Himalayas) or less (in their central parts) vast transition areas, numerous inversions or anomalies. In other words, the otherwise manifest rule "(sub)tropical organisms for (sub)tropical environments only" is

very often violated in the Himalayas, particularly in the central parts of this great mountainous land and especially as regards animals (e.g. MARTENS, 1984, 1993). Even the altitudinal zonation of Himalayan plant communities is rather conventional (DOBREMEZ, 1972) (Fig. 2).

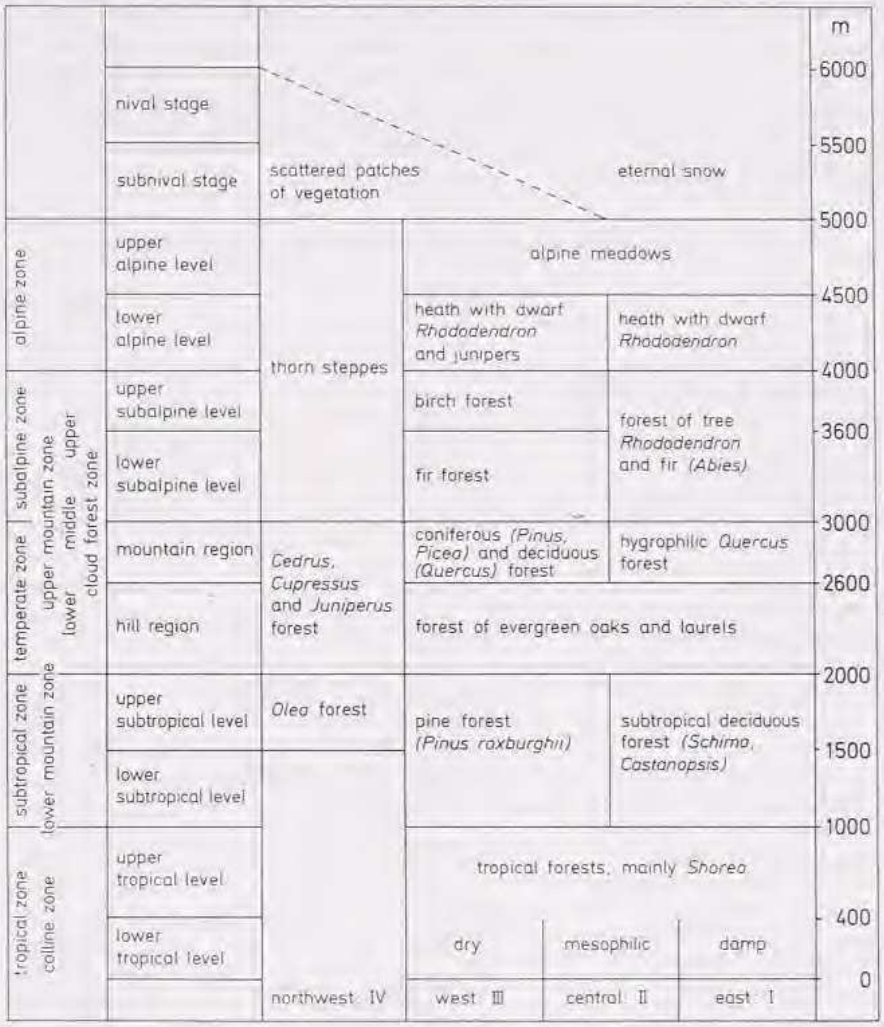

FIG. 2. — The vegetation belts and most important plant communities in the Nepal Himalayas. The Roman numerals at the bottom indicate the floral regions of Nepal (modified, after DOBREMEZ, 1972).

The present paper is the first attempt to trace the vertical distribution patterns of Himalayan millipedes which is basic for reliable faunogenetic reconstructions. This study is mainly restricted to the fauna of Nepal, the Himalayas' centralmost and particularly well-explored part, but all available information is also incorporated on the faunas of adjacent areas and of some ecologically similar soil/litter-dwelling animal groups for comparative purposes. At the start, these results must be regarded as quite preliminary, for a considerable proportion (perhaps over 50%) of the existing collections of Diplopoda remains untreated. In addition to published material, certain unpublished data are presented, chiefly derived by the senior author from the long-term research project conducted by the junior author and his collaborators since 1969 (MARTENS, 1987a; GOLOVATCH, 1990). In spite of its preliminary character, this paper seems warranted to draw some general conclusions on the patterns of diplopod faunogenesis. The latter

is the main objective, while the patterns of altitudinal distribution of Himalayan millipedes are an important tool.

DIPLOPODA OF THE HIMALAYAS

Table 1 presents all available information on the millipede fauna of, and its distribution within, the Himalayas, with over 200 species represented. However, some taxonomic remarks are necessary. A few genera are between quotation marks, for they are obscure either as taxa or as Himalayan elements (see HOFFMAN, 1980). In some cases, no information on elevations is available, this being reflected by a question mark [(?)]. Introductions (N° 183-184) are extremely rare and are referred to as synanthropic.

TABLE 1. — Geographic and vertical distribution of Himalayan diplopods.

TAXA	COUNTRY	ELEVATIONS (m.)
Order Polyxenida		
Family Polyxenidae		
Genus *Polyxenus* Latreille, 1802-03		
1. *Polyxenus* sp.	Kashmir	1585
Genus *Monographis* Attems, 1907		
2. *M. mirus* (Turk, 1947)	Kumaon	1600
Genus *Unixenus* Jones, 1944		
3. *Unixenus* sp.	Nepal	4550
Order Sphaerotheriida		
Family Sphaeropoeidae		
Genus *Indosphaera* Attems, 1936		
4. *Indosphaera curiosa* Attems, 1936	Assam	?
Genus *Kophosphaera* Attems, 1936		
5. *K. brevilamina* Attems, 1936	North Bengal, Darjeeling Distr.	1700
6. *K. devolvens* Attems, 1936	Sikkim, Darjeeling Distr.	1700-2050
7. *K. excavata* (Butler, 1874)	Nepal, Assam	?
8. *K. excavata mammifera* Attems, 1936	Darjeeling Distr., Assam	?
9. *K. politissima* Attems, 1936	Darjeeling Distr.	1700
Genus *"Sphaeropoeus"* Brandt, 1833		
10. *S. montanus* Karsch, 1881	Himalayas	?
Genus *"Sphaerotherium"* Brandt, 1833		
11. *S. maculatum* Butler, 1874	Sikkim	?
12. *S. politum* Butler, 1874	Sikkim	?
Genus *"Zephronia"* Gray, 1832		
13. *Z. alticola* Attems, 1936	Assam, Darjeeling Distr.	400-1700
14. *Z. debilis* Attems, 1936	Darjeeling Distr.	1700
15. *Z. densipora* Attems, 1936	Assam	?
16. *Z. disparipora* Attems, 1936	Assam	140
17. *Z. hirta* Attems, 1936	Darjeeling Distr.	1700
18. *Z. hysophila* Attems, 1936	Assam	?
19. *Z. juvenis* Attems, 1936	Assam	?
20. *Z. laevissima* Butler, 1874	Sikkim	?
21. *Z. lignivora* Attems, 1936	Assam	180-330
22. *Z. manca* Attems, 1936	Vietnam, Darjeeling Distr.	1000-1700
23. *Z. nigrinota* Butler, 1872	Darjeeling Distr.	2300-2700
24. *Z. specularis* Attems, 1936	Assam	?
25. *Z. tigrinoides* Attems, 1936	Darjeeling Distr.	170
26. *Z. tumida* Butler, 1882	Assam, Burma	?
27. *"Zephronia"* spp.	Nepal	250-500
Order Glomerida		
Family Glomeridae		
Genus *Hyleoglomeris* Verhoeff, 1910		
28. *H. crassipes* Golovatch, 1987	Nepal	2450-2720
29. *H. electa* Silvestri, 1917	Darjeeling Distr.	500-1700

30. *H. gorkhalis* Golovatch, 1987	Nepal	1200
31. *H. khumbua* Golovatch, 1987	Nepal	3250-3300
32. *H. modesta* Silvestri, 1917	Assam	150
33. *H. nagarjunga* Golovatch, 1987	Nepal	1900-2100
34. *H. tinjurana* Golovatch, 1987	Nepal	2450
35. *H. venustula* Silvestri, 1917	Assam	?
Order Siphonophorida		
Family Siphonophoridae		
Genus *Pterozonium* Attems, 1951		
36. *P. cingulatum* (Attems, 1936)	Vietnam, Darjeeling Distr.	500-1700
37. *P. coniceps* (Attems, 1936)	Darjeeling Distr.	1700
38. *P. larwoodi* (Turk, 1947)	Kumaon	1600
Order Platydesmida		
Family Andrognathidae		
Genus *Pseudodesmus* Pocock, 1887		
39. *?Pseudodesmus* sp.	Nepal	<2000
Order Chordeumatida		
Family Cleidogonidae		
Genus *Tianella* Attems, 1904		
40. *T. ausobskyi* Shear, 1987	Nepal	2500-3050
41. *T. bobanga* Shear, 1979	Nepal	2460-2500
42. *T. daamsae* Shear, 1987	Nepal	3600-3900
43. *T. gitanga* Shear, 1987	Nepal	2550
44. *T. jaljalensis* Mauriès, 1988	Nepal	2350
45. *T. kathmandua* Mauriès, 1988	Nepal	1700
46. *T. lughla* Shear, 1979	Nepal	2950-3300
47. *T. mananga* Shear, 1987	Nepal	2550
48. *T. mangsingma* Mauriès, 1988	Nepal	2250
49. *T. martensi* Shear, 1979	Nepal	1150-2900
50. *T. smetanai* Mauriès, 1988	Nepal	3250
51. *Tianella* sp.	Darjeeling Distr.	900-1400
Family Kashmireumatidae		
Genus *Kashmireuma* Mauriès, 1982		
52. *K. nepalensis* Mauriès, 1988	Nepal	3600-4100
53. *K. nielseni* Mauriès, 1982	Kashmir	2600-3500
54. *K. schawalleri* Shear, 1987	Nepal	3450-3600
55. *Kashmireuma* sp.	Nepal	2500-3000
Family Megalotylidae		
Genus *Nepalella* Shear, 1979		
56. *N. deharvengi* Mauriès, 1988	Nepal	2900-3500
57. *N. gairiensis* Mauriès, 1988	Nepal	3000
58. *N. gunsa* Shear, 1987	Nepal	3600-3800
59. *N. jaljalae* Mauriès, 1988	Nepal	2200
60. *N. khumbua* Shear, 1979	Nepal	3250-3300
61. *N. phulcokia* Mauriès, 1988	Nepal	2250
62. *N. ringmoensis* Mauriès, 1988	Nepal	2750-3000
63. *N. taplejunga* Shear, 1987	Nepal	3000-3300
64. *N. thodunga* Shear, 1979	Nepal	3200
65. *N. tragsindola* Mauriès, 1988	Nepal	2450-3000
66. *Nepalella* sp.	Nepal	1900-4100
Order Julida		
Family Julidae		
Genus *Anaulaciulus* Pocock, 1895 (cf. KORSÓS, 1996)		
67. *A. acaudatus* Korsós, 1996	Sikkim	3990
68. *A. bilineatus* Korsós, 1996	Nepal	3300-4300
69. *A. kashmirensis* Korsós, 1996	Kashmir	3100-3200
70. *A. nepalensis* Korsós, 1996	Nepal	2600-3400
71. *A. niger* Korsós, 1996	Nepal	2600-4500
72. *A. tibetanus* Korsós, 1996	China (E-Tibet), Assam	3700
73. *A. topali* Korsós, 1996	Kashmir	2300

Genus *Nepalmatoiulus* Mauriès, 1983		
74. *N. appendiculatus* Enghoff, 1987	Kumaon	1900-2100
75. *N. deharvengi* (Mauriès, 1983)	Nepal	2550-3350
76. *N. dhaulagiri* Enghoff, 1987	Nepal	3000-3350
77. *N. generalis* Enghoff, 1987	Nepal	3400
78. *N. hyalilobus* Enghoff, 1987	Nepal	3600-3800
79. *N. ivanloebli* Enghoff, 1987	Nepal	2200-4800
80. *N. juxtapositus* Enghoff, 1987	Nepal	2800-3050
81. *N. martensi* Enghoff, 1987	Nepal	3250-3300
82. *N. mauriesi* Enghoff, 1987	Nepal	3600
83. *N. nigrescens* Enghoff, 1987	Bhutan	2300
84. *N. pineti* Enghoff, 1987	Nepal	2900
85. *N. rugiflagrum* Enghoff, 1987	Bhutan	3300
86. *N. smetanai* (Mauriès, 1983)	Nepal	1900-2700
87. *N. sympatricus* Enghoff, 1987	Nepal	3000
88. *N. uncus* Enghoff, 1987	Nepal	2550
89. *N. wuermlii* Enghoff, 1987	Bhutan	1680-2600
90. *N. zachonoides* Enghoff, 1987	Nepal	2450-2600
Order Spirostreptida		
Family Harpagophoridae		
Genus *Gonoplectus* Chamberlin, 1921		
91. *G. alius* Demange, 1961	Assam	?
92. *G. bhutanensis* Demange, 1988	Bhutan	350-450
93. *G. broelemanni* Demange, 1961	Nepal	1800-2300
94. *G. corniger* (Attems, 1936)	Assam	?
95. *G. gracilis* (Attems, 1936)	Darjeeling Distr.	1200
96. *G. hyatti* Demange, 1961	Nepal	1200
97. *G. lindbergi* Demange, 1961	Darjeeling Distr., Bhutan	350
98. *G. malayus* (Carl, 1909)	Kumaon, Nepal, Bhutan	200-2500
99. *G. probus* (Attems, 1936)	Darjeeling Distr.	1000
100. *G. remyi* Demange, 1961	Assam	?
101. *G. sulcatus* (Attems, 1936)	Darjeeling Distr.	2400
Order Cambalida		
Family Cambalopsidae		
Genus *Podoglyphiulus* Attems, 1909		
102. *P. elegans nepalensis* Mauriès, 1983	Nepal	<1000
Genus *Trachyjulus* Peters, 1864		
103. *T. mimus* Silvestri, 1924	Assam	1200
104. *T. wilsonae* Mauriès, 1983	Nepal	<1000
Order Spirobolida		
Family Physobolidae		
Genus *Physobolus* Attems, 1936		
105. *P. olivaceus* Attems, 1936	Darjeeling Distr.	1800.
Order Polydesmida		
Family Cryptodesmidae		
Genus *Trichopeltis* Pocock, 1894		
106. *T. watsoni* Pocock, 1894	Darjeeling Distr., Assam, Bhutan, West Bengal, Bangladesh	350-1000
Family Fuhrmannodesmidae		
Genus *Assamodesmus* Manfredi, 1954		
107. *A. lindbergi* Manfredi, 1954	Assam	?
Genus *Hingstonia* Carl, 1935		
108. *H. beatae* Golovatch, 1990	Nepal	2400-3500
109. *H. dorjulana* Golovatch, 1988	Bhutan	2450-3100
110. *H. eremita* Carl, 1935	Nepal	2000
111. *H. falcata* Golovatch, 1986	Nepal	2650
112. *H. fittkaui* Golovatch, 1990	Nepal	3550-3650
113. *H. gogonana* Golovatch, 1988	Bhutan	3650-4000
114. *H. pahakholana* Golovatch, 1990	Nepal	2600-2800
115. *H. pelelana* Golovatch, 1988	Bhutan	3300-3400
116. *H. perarmata* Golovatch, 1986	Nepal	3150

117. *H. serrata* Golovatch, 1987	Nepal	3400-3600
118. *H. sympatrica* Golovatch, 1990	Nepal	3550-3650
119. *H. variata* Golovatch, 1987	Nepal	2600-4500
120. *Hingstonia* sp.	Nepal	2200-3900
Genus *Magidesmus* Golovatch, 1988		
121. *M. affinis* Golovatch, 1988	Bhutan	3300-3400
122. *M. bhutanensis* Golovatch, 1988	Bhutan	3100
Genus *Sholaphilus* Carl, 1932		
123. *S. asceticus* Golovatch, 1986	Nepal	1300-1650
124. *S. dalai* Golovatch, 1986	Nepal	2400
125. *S. gompa* Golovatch, 1990	Nepal	2000-2100
126. *S. lama* Golovatch, 1986	Nepal	1800-2000
127. *S. martensi* Golovatch, 1986	Nepal	1100-1850
128. *S. monachus* Golovatch, 1990	Nepal	2050-2150
Genus "*Pseudosphaeroparia*" Carl, 1932		
129. *P. cavernicola* Turk, 1945	Kumaon	2800
Genus *Topalodesmus* Golovatch, 1988		
130. *T. communis* Golovatch, 1988	Darjeeling Distr.	2000-2200
Family Polydesmidae		
Genus *Bhutanodesmus* Golovatch, 1988		
131. *B. velatus* Golovatch, 1988	Bhutan	350-450
Genus *Glenniea* Turk, 1945		
132. *G. bhotiaensis* Golovatch, 1988	Bhutan	350-450
133. *G. indica* Turk, 1945	Kumaon	2800
134. *G. minuscula* Golovatch, 1988	Bhutan	1900-2300
135. *G. perarmata* Golovatch, 1988	Bhutan	1680
136. *G. martensi* (Golovatch, 1987)	Nepal	1200
Genus *Himalodesmus* Golovatch, 1986		
137. *H. audax* Golovatch, 1986	Nepal	2650
138. *H. benefactor* Golovatch, 1987	Nepal	2600-3400
139. *H. faustus* Golovatch, 1987	Nepal	1000-1750
140. *H. parvus* Golovatch, 1987	Nepal	2200
141. *H. prosperus* Golovatch, 1990	Nepal	2600-2800
142. *H. pulcher* Golovatch, 1987	Nepal	2450
143. *H. pygmaeus* Golovatch, 1986	Nepal	3300-3400
144. *H. vigens* Golovatch, 1987	Nepal	2150-2250
Genus *Typhlopygmaeosoma* Turk, 1972		
145. *T. hazeltonae* Turk, 1972	Kumaon	1850
Genus *Usbekodesmus* Lohmander, 1932		
147. *U. buddhis* Golovatch, 1986	Nepal	3300-3400
148. *U. occultus* Golovatch, 1986	Nepal	2300-2800
149. *U. sacer* Golovatch, 1987	Nepal	3300-3400
150. *U. theocraticus* Golovatch, 1990	Nepal	2600-2800
151. *U. theosophicus* Golovatch, 1986	Nepal	3200
152. *Usbekodesmus* sp.	Nepal, Bhutan	3450-4250
Family Opisotretidae		
Genus *Martensodesmus* Golovatch, 1987		
153. *M. bicuspidatus* Golovatch, 1988	Bhutan	1650-2000
154. *M. excornis* Golovatch, 1988	Bhutan	2440
155. *M. himalayensis* Golovatch, 1987	Nepal	1100-1300
156. *M. nagarjungicus* Golovatch, 1987	Nepal	1900-2100
157. *M. sherpa* Golovatch, 1987	Nepal	1200
158. *Martensodesmus* sp.	Nepal, Bhutan	1300-2150
Family Paradoxosomatidae		
Genus *Armolites* Golovatch, 1984		
159. *A. chulingensis* Golovatch, 1994	Nepal	3000-3700
160. *A. communicans* Golovatch, 1992	Nepal	2650
161. *A. similis* Golovatch, 1992	Nepal	2300-2700
162. *A. spiniger* (Attems, 1936)	Darjeeling Distr.	1000-2200
Genus *Hirtodrepanum* Golovatch, 1994		
163. *H. latigonopum* Golovatch, 1994		

Genus *Kaschmiriosoma* Schubart, 1935		
164. *K. contortipes* Schubart, 1935	Kashmir, N-Pakistan	2300-3300
165. *K. nulla* (Attems, 1936)	Himachal Pradesh	1000
166. *K. pleuroptera* (Attems, 1936)	Punjab (Pakistan)	2800
Genus *Kronopolites* Attems, 1914		
167. *K. occidentalis* Golovatch, 1983	Kashmir	1500
Genus *Martensosoma* Golovatch, 1992		
168. *M. elegans* Golovatch, 1992	Nepal	1350
169. *M. foveatum* Golovatch, 1992	Nepal	1800-2000
170. *M. schawalleri* Golovatch, 1992	Nepal	1000-2150
171. *M. silvestre* Golovatch, 1994	Nepal	2000-2600
172. *M. splendens* Golovatch, 1992	Nepal	1650-2150
173. *M. unicolor* (Attems, 1936)	Assam, Darjeeling Distr.	1200-1700
Genus *Nepalomorpha* Golovatch, 1993		
174. *N. arunensis* Golovatch, 1994	Nepal	1850-2150
175. *N. hirsuta* Golovatch, 1994	Nepal	3900-4100
176. *N. kuznetsovi* Golovatch, 1994	Nepal	3000
177. *N. spinigera* (Golovatch, 1992)	Nepal	600-1400
Genus *Orophosoma* Jeekel, 1980		
178. *O. fechteri* Golovatch, 1990	Nepal	2330-3150
179. *O. hingstoni* (Carl, 1935)	Tibet	3400
180. *O. simulans* (Carl, 1935)	Nepal, Tibet	3700
181. *Orophosoma* sp.	Nepal	1750-3450
Genus *Orthomorpha* Bollman, 1893		
182. *"O." almorensis* Turk, 1947	Kumaon	1600
183. *O. coarctata* (Saussure, 1860)	Nepal (synanthr.)	600-650
Genus *Oxidus* Cook, 1911		
184. *O. gracilis* (C. L. Koch, 1847)	Nepal (synanthr.)	570-1200
Genus *Paranedyopus* Carl, 1932		
185. *P. affinis* Golovatch, 1990	Nepal	2475-2700
186. *P. cylindricus* (Carl, 1935)	Nepal, Darjeeling Distr.	1650-2850
187. *P. elongissimus* Golovatch, 1984	Darjeeling Distr.	1000
188. *P. martensi* Golovatch, 1990	Nepal	2250-3600
189. *P. schawalleri* Golovatch, 1990	Nepal	2050-2150
190. *P. similis* Golovatch, 1990	Nepal	2300-3000
191. *Paranedyopus* sp.	Nepal	2450-2900
Genus *Parorthomorpha* Golovatch, 1994		
192. *P. affinis* Golovatch, 1994	Nepal	1400
193. *P. granulosa* Golovatch, 1994	Nepal	2000
194. *P. intermedia* Golovatch, 1994	Nepal	1000-1100
195. *P. longiseta* Golovatch, 1994	Nepal	1400-1600
196. *P. nyakensis* (Golovatch, 1992)	Nepal	2270-2450
197. *P. philosophica* Golovatch, 1994	Nepal	1650-2450
198. *P. spectabilis* Golovatch, 1994	Nepal	2650
199. *P. tergalis* Golovatch, 1994	Nepal	2650
200. *P. tuberculata* Golovatch, 1994	Nepal	3000-3300
Genus *Substrongylosoma* Golovatch, 1984		
201. *S. distinctum* Golovatch, 1984	Darjeeling Distr.	1200-1500
202. *S. falcatum* Golovatch, 1984	Darjeeling Distr.	1400
203. *S. montigena* (Carl, 1935)	Darjeeling Distr.	1200-2300
204. *S. schawalleri* Golovatch, 1993	Nepal	1620-2000
Genus *Topalosoma* Golovatch, 1984		
205. *T. setiferum* Golovatch, 1984	Darjeeling Distr.	900
Genus *Touranella* Attems, 1937		
206. *T. himalayaensis* Golovatch, 1994	Nepal	2300-2700
Family Pyrgodesmidae		
207. Several genera and species	Nepal	450-1200

ZOOGEOGRAPHIC PATTERNS

The vast majority of Himalayan millipede species are local in distribution; there are few relatively widespread species like *Trichopeltis watsoni*. Indeed, most Himalayan millipede species are known from a single locality only, and many others appear to be restricted not only in area, but also in altitude.

Conversely, most genera occur through a range of altitudes, as shown in Figure 3, but are more or less restricted to forests, demonstrating sylvicoly. Table 1 and Figures 2-3 show that the alpine zone of the Central Himalayas is only marginally populated by millipedes, whereas the tropical and subtropical forest belts support the bulk of the fauna. This pattern conforms to general knowledge that millipedes are primarily a class of forest floor-dwellers, which in temperate regions of Eurasis seems trophecologically and historically associated with nemoral (= broadleaved) forest communities (GOLOVATCH, 1987, 1991a). In turn, this pattern provides the basis for faunogenetic reconstructions based on phyto- and paleogeographic evidence.

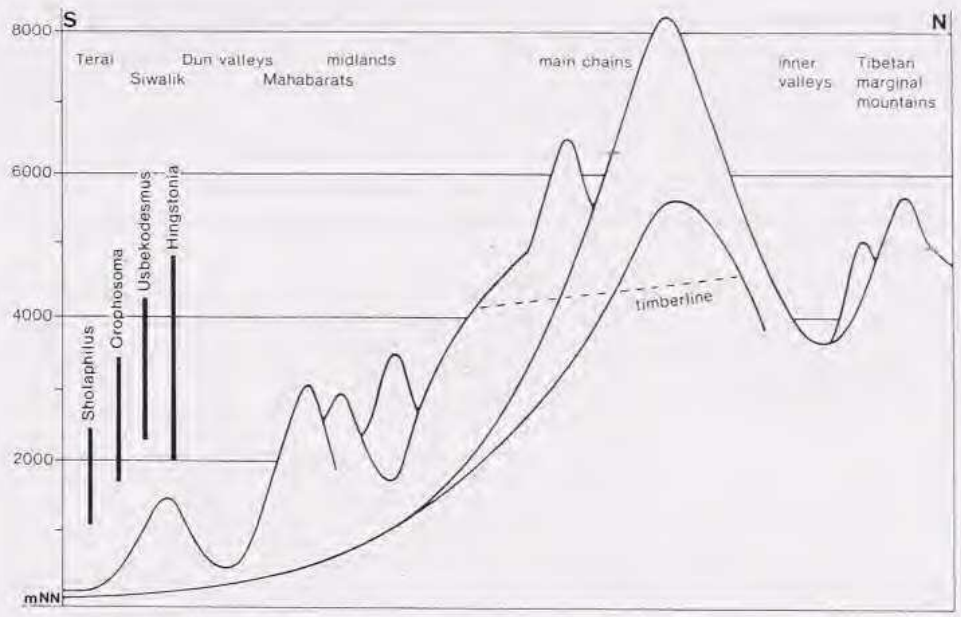

FIG. 3. — Vertical distribution of some millipede genera in the Central Himalayas - genera *Usbekodesmus*, *Hingstonia*, *Sholaphilus*, *Orophosoma*.

From the primary immigration routes of invertebrate and vertebrate faunal components in the Central Himalayas, MARTENS (1984, 1993) distinguished Central Asian, West Asian Himalayan, Tropical Indian, West Chinese Himalayan, and Indochinese Himalayan pathways (Fig. 4). However, because of their preponderance in forests, only two major dispersal routes are available to the Diplopoda, from Southeast Asia and the Indian subcontinent. Consequently, the millipede fauna of the Central Himalayas is dominated by such tropical elements as the families Sphaeropoeidae, Siphonophoridae, Andrognathidae, Harpagophoridae, Cambalopsidae, Physobolidae, Cryptodesmidae, Opisotretidae, Fuhrmannodesmidae, Paradoxosomatidae, Pyrgodesmidae, etc., which have Oriental and/or Indian affinities. In the relatively well-explored Central Himalayas, most millipede species are restricted to tropical lowland forests such that it is difficult to discriminate Southeast from Indian derivatives. Possibly only *Sholaphilus*, *Trichopeltis* and certain Sphaeropoeidae hold eutropical Indian origins.

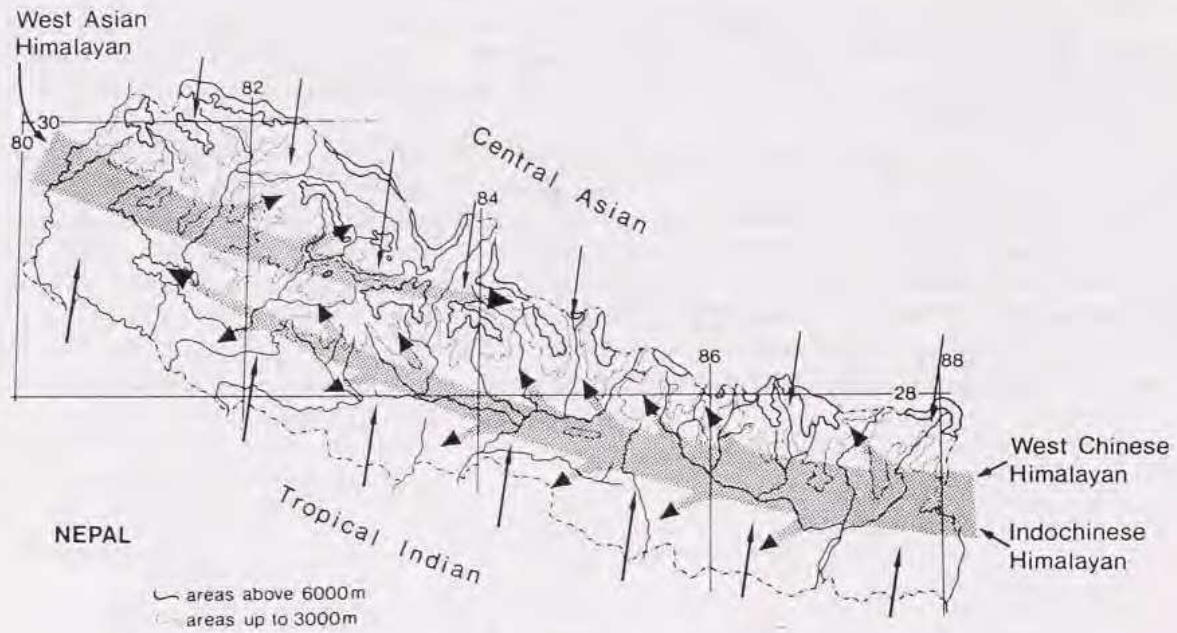

FIG. 4. —The main immigration routes of faunal components into the Nepal Himalayas.

Such genera as *Hyleoglomeris*, *Tianella*, *Anaulaciulus*, and *Usbekodesmus* are primarly Palearctic and are restricted in the Central Himalayas to the uppermost forests, some even spreading into alpine meadows above 4,000 m a.s.l., which contrasts with nearly 6,000 m for certain other terrestrial invertebrates, e.g. spiders (MARTENS, 1993). The highest millipede record in the Himalayas, and probably also in the world, is of *Nepalmatoiulus ivanloebli* (ENGHOFF, 1987) encountered at 4,800 m a.s.l. Other millipedes demonstrate subtropical east and southeast Asian elements, although there are occasional exceptions to the general rule, "(sub)tropical creatures in (sub)tropical environments only". Families that are more subtropical than tropical include the Kashmireumatidae (with the oligotypic genus, *Kashmireuma*, in the Himalayas and another monobasic genus in Vietnam), Megalotylidae (with the Oriental genus *Nepalella* and a monobasic genus in the Russian Far East), Julidae (with *Anaulaciulus* and the Oriental highly prolific genus *Nepalmatoiulus*), and certain Fuhrmannodesmidae and Paradoxosomatidae [e.g., the endemic genera *Hingstonia* and *Orophosoma* (Fig. 3)].

The border between subtropical and purely tropical Himalayan components seems to be vague (MARTENS, 1984, 1987b, 1993), as is that between forest (sub)zones (Fig. 2). Only a few genera and even fewer tribes and families display clear vertical distribution patterns. In most species there are only slight correlations with particular elevations. Some closely related genera and species tend to occupy different altitudinal zones, probably because of niche segregation. For example, *Hingstonia* and *Sholaphilus* (Fuhrmannodesmidae) tend to inhabit upper and lower forests, respectively (Fig. 3), and this pattern is better demonstrated within speciose genera. *Usbekodesmus*, for example, tends to be restricted to the upper forest belt, but a few components are confined to low elevations, between 2,300 and 4,250 m a.s.l. (Table 1, Fig. 3).

The same patterns have been reported for spiders, harvestmen, insects, birds, etc. (MARTENS, 1984, 1987b, 1993), but the Diplopoda is distinguished in being almost strictly sylvicolous and virtually entirely Oriental and/or Indian in origin.

The classical pattern of a prolonged cis-Himalayan band west of Brahmaputra, marking the northwesternmost border of the Oriental realm, is highly characteristic of Oriental Diplopoda

(HOFFMAN & BURKHALTER, 1978), and most Himalayan genera and tribes demonstrate this pattern. An Oriental influence dominates in Kashmir, which is the classics, but also, unexpectedly, to the north beyond the Indus Valley. Thus, judging from millipedes "...the less elevated and more mild areas of modern North Pakistan seem to have retained particularly ancient faunal elements as compared to the adjacent extremely high and severe Himalayas nowadays supporting only relatively more advanced, younger forms" (GOLOVATCH, 1991a: 876).

FAUNOGENESIS

As the regional phyto- and paleogeography are well documented (WULFF, 1944; MEYEN, 1987), one can reasonably surmise that the Himalayas have served as a dispersal pathway for a uniform Turgai biota (e.g. *Quercus*, *Pyrus*, *Malus*, and deciduous tree genera and associated faunas) during the early and mid-Tertiary, which spread northwestward along the receding southern coast of the Tethys Sea. A very considerable proportion of present-day European and Mediterranean millipede genera, tribes, and families also seem to reflect repeated northwestward dispersals from source areas in East and/or Southeast Asia, for example *Hyleoglomeris* and possibly the Glomeridae as a whole, the tribes Brachyiulini and Leucogeorgiini (Julidae), the tribe Paradoxosomatini and possibly all Paradoxosomatidae, and the genus *Polydesmus* and possibly all Polydesmidae (GOLOVATCH, 1987, 1991a, 1991b, 1993).

Beyond their effects on areas to the northwest, the Himalayas have also been a center of secondary diversification since the Plio-Pleistocene, and much of the Central and West Himalayas seem to have experienced a pronounced, secondary faunal impoverishment (GOLOVATCH, 1991a), because all endemic millipedes display a relatively low taxonomic rank. The development of local species swarms (among *Tianella*, *Nepalella*, *Anaulaciulus*, *Nepalmatoiulus*, *Gonoplectus*, *Hingstonia*, *Himalodesmus*, *Paranedyopus*, etc.) through allopatric speciation is a prominent characteristic of Himalayan Diplopoda irrespective of origin, as has been observed among other soil/litter arthropods (MARTENS, 1987b, 1993). The few anthropochorous introductions are very recent and have failed to alter the general zoogeographic pattern of Himalayan Diplopoda.

Although preliminary, these reconstructions provide a basis for comparisons for future faunistic and zoogeographic studies of the Himalayas. Compared to other terrestrial Arthropoda (MARTENS, 1993), the salient aspects of Himalayan Diplopoda are pronounced sylvicoly and Oriental and/or Indian origin, and their ostensible Palearctic influence also originates in present-day subtropical regions of Southeast and East Asia.

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